

## CHROMOSOME RELATIONSHIPS IN THE POMOIDEAE

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*With plate 50*

THE ROSACEAE include four tribes or subfamilies which "are all closely linked together by their floral characters" (Rehder 1927.) The basic chromosome numbers are 8 and 9 in the Spiraeoideae, 7 and 9 in the Rosoideae, 8 in the Prunoideae, but it is 17 in all the genera of the Pomoideae. Polyploidy is found in all of these subfamilies although in the Pomoideae it is limited to triploids and tetraploids with very few exceptions.

According to Darlington and Moffett (1930) the 17 pairs of chromosomes in *Pyrus* are made up from a basic number of 7 by a duplication of 4 pairs and a triplication of 3 pairs of chromosomes. The Pomoideae are considered as complex autopolyploids and their morphological characters are attributed to this reorganization of the 7 basic chromosomes. These conclusions are based on the fact that there is a tendency for the chromosomes to be associated in groups of two or three pairs at meiosis and the fact that the basic chromosome is 7 in the more important genera of the Rosoideae. These authors also describe quadrivalent and sexivalent chromosomes at meiosis in diploid species.

The writer (Sax, 1931) and Moffet (1931a, 1931b) have found that all genera of the Pomoideae have 17 chromosomes as the basic number. The different genera are closely allied as shown by their morphological characters and their breeding and grafting relationships. They have undoubtedly had a common origin and the chromosome behavior should be similar in all genera.

In most genera there is a tendency for the bivalents to be grouped in the first meiotic division, but different genera seem to vary in this respect. The chromosomes of *Crataegus* and *Cotoneaster* do show secondary association to such an extent that consistent counts are difficult, but in *Sorbus*, *Aronia* and *Amelanchier* the 17 chromosomes of diploid species are well differentiated in most cases, although there is some evidence of secondary association.

The interpretation of the quadrivalent and sexivalent associations in diploid species may well be questioned. In most cases the multivalent "pairing" shown by Darlington and Moffett is based on the apparent contact between chromosome strands at late metaphase, although one diakinesis figure (text-fig. 11) is shown with one sexivalent, four quadrivalents and six bivalents. The con-



necting strands at late metaphase are about .05 micron in diameter and the difficulty in following these strands in side views in a metaphase figure containing 17 chromosomes makes any conclusions concerning multivalent associations rather questionable. It is probably significant that "multivalent" associations from side views were found far less frequently than those derived from polar views.

Later investigations by Moffett (1931b) show that there is little, if any, real multivalent pairing in diploid Pomoideae. At diakinesis he found that "in the great majority of divisions examined 17 bivalents were observed." The occasional "quadrivalents" shown in diploid species probably do not represent true pairing of four chromosomes but is simply a grouping of two bivalents due to secondary association.

If the Pomoideae are autopolyploids with sufficient homology and chiasma formation to permit multivalent chromosome association, the chromosomes in a triploid should form either multivalents or bivalents or both, but few if any univalents. There is, however, a large proportion of univalents in triploids. Only two or three univalents were found at metaphase in *Pyrus* by Darlington and Moffett, but at anaphase as many as 9 were found. In *Pyrus minima* (= *Sorbus minima*), Moffett shows as many as 12 to 15 univalents at metaphase and anaphase. The number of lagging univalents at anaphase is undoubtedly a better index of chromosome association than counts made at earlier stages, and simply confirms the conclusion that the multivalent associations found in diploids do not represent true pairing of chromosomes.

The writer has studied several triploid forms in the Pomoideae and has found a large proportion of univalents in all cases. *Sorbaronia alpina*, a hybrid between *Sorbus Aria* and *Aronia arbutifolia* (Rehder 1926), is a triploid. Judging from the appearance of this tree it has two sets of *Sorbus* chromosomes and one set of *Aronia* chromosomes. At the first meiotic division there are about 17 bivalents or trivalents and from 6 to 15 univalents. Polar views of the first meiotic division are shown in Figures 1 and 2. The univalents are usually found around, or at one side of, the bivalents and trivalents and usually not in the same plane as shown in the side views. (Figs. 3 and 4.) It is not possible to distinguish between bivalents and trivalents in polar views and even from side views of the division figure the trivalents are not easily differentiated. There are, however, usually 17 pairs or multivalent associations of chromosomes so that the deficiency of univalents must be accounted for on the assumption that some trivalents are formed.



A few trivalent chromosomes can be observed from side views. If pairing occurs between the extra 17 chromosomes we would expect about 24 bivalent chromosomes and one univalent. At anaphase the univalents lag behind and ultimately divide. The most usual number of lagging univalents found is 11 or 12. (Figs. 5 and 6.) This observation is in accord with the numbers found at metaphase.

*Sorbopyrus auricularis bulbiformis* is also a triploid and as previously described (Sax 1931) it has about 12 univalents at the first meiotic division. (Fig. 7.)

*Malus theifera* is another triploid which shows some univalents at the first meiotic division. (Fig. 8.) The divisions in the pollen mother cells are very irregular and practically no pollen grains are found in the mature anthers. The division in the megaspore mother cell is more regular and apparently trivalents are formed with only an occasional univalent chromosome. This species sets an abundant crop of fruit, the seeds are fertile and the seedlings are all true to type. The fact that this species is a triploid and has no functional pollen, but breeds true from seed, indicates that apomictic development occurs. The details of embryo origin and development have not yet been determined.

The evidence from triploid Pomoideae clearly indicates that there is little or no pairing among the extra 17 chromosomes and that this subfamily is not an autopolyploid with a basic number of 7 chromosomes. There is of course the possibility of autopolyploid origin so early that the originally homologous chromosomes have been so differentiated that they now show only weak affinities. But the Pomoideae are apparently of comparatively recent origin as indicated by the fertility of species and even generic hybrids, and the comparative morphology of the different genera.

It seems much more probable that the Pomoideae are allopolyploids derived from parental types with 8 or 9 chromosomes. In all other subfamilies of the Rosaceae the basic chromosome numbers for almost all genera are 7, 8, or 9. In the Spiraeoideae the basic number is 8 for *Spiraea* and *Exochorda* and 9 for *Physocarpus*, *Pentactina*, and *Sibiraea*. Hexaploid species have been found in *Spiraea*.

In the Rosoideae the basic chromosome numbers are 7 and 9. The larger genera such as *Rosa*, *Rubus* and *Potentilla* have a basic number of 7 chromosomes, but the monotypic genera *Rhodotypus*, *Kerria* and *Neviusia* each have 9 pairs of chromosomes. (Figs. 9, 10, 11.) The writer (Sax 1931) previously reported 8 pairs of chromosomes in *Rhodotypus* and *Neviusia*, but there are apparently 9 pairs. The fact that two pairs may be so closely associated that



counts are difficult suggests that some chromosome duplication may have occurred in these genera. If the Pomoideae have been derived from other subfamilies in the Rosaceae, it would seem that the Spiraeoideae and Rosoideae were involved. My colleague Mr. Rehder tells me that the Pomoideae are taxonomically more closely allied to the Spiraeoideae than to either of the other two subfamilies. Crosses between earlier types of Spiraeoideae or perhaps between primitive forms of Spiraeoideae and Rosoideae may have been the basis for the origin of the Pomoideae. Hybrids between forms close enough to cross would indicate some chromosome homologies although perhaps not close enough for chromosome pairing. Doubling of the chromosome number in the  $F_1$  hybrid would insure fertility and an allotetraploid would be produced with 17 chromosomes. The recent production of allotetraploids in different families shows that such an origin of a new type of plant is quite possible.

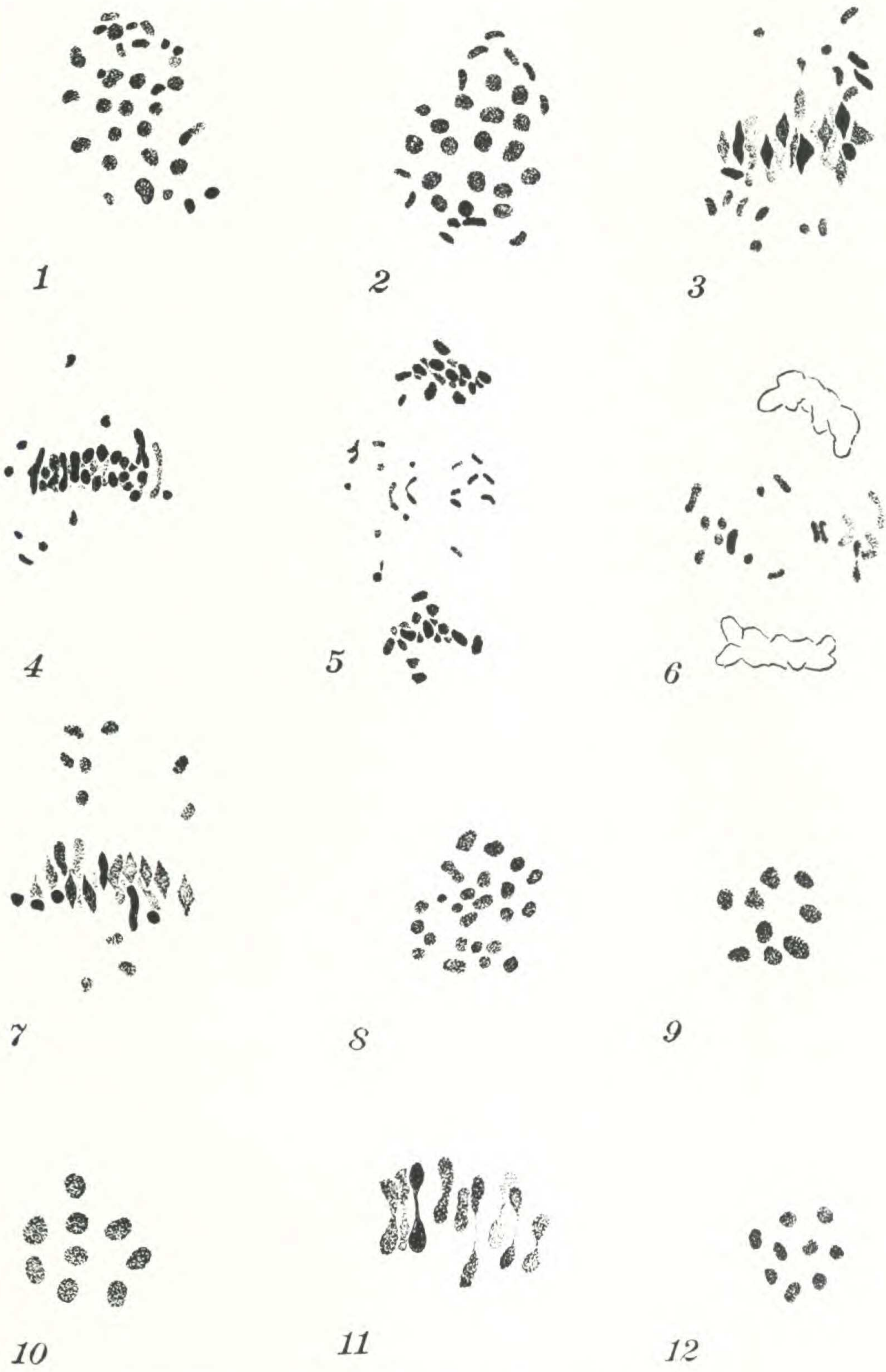
In such an allotetraploid there might well be sufficient affinities to produce some secondary pairing of bivalent chromosomes although real pairing to form quadrivalents would rarely or never occur. Some secondary pairing may have been present in one of the contributing diploids as suggested by the chromosome behavior in *Rhodotypus* and *Neviusia*. Lawrence (1931) has presented good evidence that secondary association of bivalents does occur in many genera, apparently due to remote affinities between chromosomes which are too well differentiated to permit multivalent chromosome pairing. As Lawrence points out such allopolyploids would have a high survival value due to hybrid vigor and a high degree of fertility. The differentiation of genera and species within the Pomoideae can be attributed primarily to mutations or minor changes in the 17 pairs of chromosomes.

#### SUMMARY

*Sorbaronia alpina*, *Sorbopyrus auricularis* and *Malus theifera* are triploids. At the first meiotic division in the pollen mother cells there are about 17 bivalents and trivalents, and from 6 to 15 univalent chromosomes. The fact that about 12 univalents are usually found in triploid forms of Pomoideae shows that this subfamily is not an autopolyploid with a basic number of 7 chromosomes as several writers have suggested.

The basic chromosome numbers in the other subfamilies of the Rosaceae are 7, 8, and 9. The Pomoideae may have originated from one or perhaps two of these subfamilies by hybridization between different primitive forms followed by chromosome doubling





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